

THE GENERA OF THE TRIBE HYDROPHYLLAE OF  
THE HYDROPHYLLACEAE

LINCOLN CONSTANCE

A systematic study of *Nemophila*, which was undertaken with the objective of offering yet another revision of that genus, revealed not only difficulties in delimiting the species but also that lines traditionally accepted to separate the genera of the tribe Hydrophyllae did not, in certain cases, conform to natural boundaries. Hence, the study was broadened to include all those plants which have customarily been referred to the tribe, but concerned itself especially with *Ellisia* and *Nemophila*. The facts appear to necessitate a general realignment of these genera before monographic treatments of the several groups of species can be profitably presented.

Asa Gray (7) was the first writer to organize the three genera, *Hydrophyllum* L., *Ellisia* L. and *Nemophila* Nutt., into the tribe Hydrophyllae. He characterized the group principally by the possession of a unilocular ovary, largely filled at certain stages of development by two large fleshy parietal placentae, upon which the ovules are produced, and also by the presence of a single, more or less bifid style. This definition of the tribe has remained substantially unchanged to the present time, and is so accepted by Bentham and Hooker (4), Peter (15) and Brand (5). Some species have been removed by certain authors from each of the three genera under the segregates, *Eucrypta* Nutt., *Decemium* Raf. and *Pholistoma* Lilja, but conservative botanists have, in the main, retained not only the tribal grouping but also the three classical genera. The substitution of *Macrocalyx* Trew and *Nyctelea* Scop. for *Ellisia* and of *Viticella* Mitch. for *Nemophila* was based upon purely nomenclatorial considerations and can be disregarded in this discussion inasmuch as *Ellisia* has been conserved and *Nemophila* is on the list of *nomina generica conservanda proposita*. *Nemophila* has been in common use for more than a century and its retention also is to be advocated in the interest of nomenclatorial stability.

*Hydrophyllum*, distinguished by its perennial or biennial habit, usually basal but always alternate leaves, many-flowered, semi-scorpoid and usually congested inflorescence and exerted stamens, has been little confused with either of the other two genera, which are annual with chiefly cauline leaves and usually at least the lowest pair opposite, while the flowers are solitary or few in loose, raceme-like cymes and the stamens are included. Brand (5) has taken up *Decemium* (treated by Gray as a section of *Hydrophyllum*) and has constituted it a monotypic genus based upon *H. appendiculatum* Michx., which differs from members of section *Euhydrophyllum* Gray chiefly in possessing appendaged calyx-sinuses, an accrescent calyx, a biennial habit and only

slightly exerted stamens. Because of the sporadic occurrence of these calycine conditions without close conformance to natural generic lines elsewhere in the tribe, and because the other two features appear to be scarcely of generic importance, it would seem advisable to retain this species within *Hydrophyllum*.

Various sets of characters have been drawn into service to distinguish *Ellisia* from *Nemophila*, but the difference most commonly emphasized—and the only one employed by Brand (5) in his generic key—is the presence in *Nemophila* of appendaged calyx-sinuses, as opposed to the absence of any such auricles in *Ellisia*. This lack of appendages on the calyx, indeed, is the only feature, save tribal similarities, possessed in common by all the species usually combined into *Ellisia*. Bentham (3), who first contrasted *Ellisia* with *Nemophila*, laying chief emphasis upon the presence or absence of auricles, clearly questioned the value of this distinction in the following words:

“. . . in some instances the sinuses (as in some Campanulaceae) are furnished with reflexed appendages, resembling the erect divisions of the calyx in form, but smaller in size. . . . these divisions do not indicate any organic modifications in the composition of the calyx, but are merely owing to the prolongation of the united lateral nerves of two adjoining sepals. . . . The character derived from this circumstance must consequently be inconstant, and have little or no relation to general habit . . . and, if that be really the only distinction between *Nemophila* and *Ellisia*, it proves the expediency of uniting these two genera . . . *Nemophila* and *Ellisia*, when taken together, are a natural group, but are separated by a purely artificial character.”

However, Bentham kept the genera separate in this and in a later (4) treatment. The two genera were actually merged by Baillon (2) who, without comment but doubtless influenced by Bentham's remarks, placed all the species of *Nemophila* under *Ellisia*, but did not make the necessary nomenclatorial recombinations. Chandler (6), in his excellent revision of *Nemophila*, noted that, “The question of the relation of *Nemophila* to *Ellisia* is vital, but must be left for future consideration.”

The auricles of certain species of *Nemophila*, particularly *N. pulchella*, are frequently obsolete, so that Brand (5) cited under both genera specimens referable to this one species. Many specimens of *Ellisia Nyctelea*, type species of its genus, show occasional sepaloid teeth which are scarcely distinguishable from auricles.

Additional distinctions which have been used to separate the two genera are these: (1) the non-enlargement of the fruiting-calyx in *Nemophila*, its marked accrescence in *Ellisia*; (2) the presence of a deciduous cap of colorless cells (the “caruncle,” “calyptra” or “cucullus”) at the chalazal end of the mature seed in *Nemophila*, its complete absence in *Ellisia*; (3) the presence of corolla-scales in *Nemophila*, a pair at the base of each filament, as opposed to their obsolescence or absence in *Ellisia*; and (4) the fact that the corolla usually exceeds the calyx in *Nemophila* but

is shorter than the calyx in *Ellisia*. A detailed consideration of this formidable array of differences, however, leads to the discovery of important contradictions in all of them.

The calyx of *Nemophila breviflora*, *N. Kirtleyi* and *N. phacelioides*, especially, is more strongly accrescent than that of *Ellisia chrysanthemifolia* or *E. micrantha*, whereas the calyx of all species of both genera enlarges to some degree in fruit. *Nemophila aurita* and *N. racemosa* entirely lack the distinguishing cucullus on the seed, and that on the seed of *N. breviflora*, *N. microcalyx* and *N. phacelioides* is reduced and persistent. The interstaminal scales in species of *Ellisia* are often more conspicuous than the squamae in certain collections of *Nemophila*, many of whose species have forms with the scales reduced to pubescent lines or quite obsolete. The corolla of *N. breviflora* is definitely shorter than the calyx, that of *N. parviflora*, *N. pedunculata* and varieties of *N. pulchella* often scarcely exceeds it, and that of *Ellisia membranacea* and *E. chrysanthemifolia* is distinctly longer than the calyx. None of these characters, then, is without striking exceptions which would seem to diminish the height of the traditional generic barriers.

Whereas *Nemophila* has not been sectionally divided by anyone, its members usually being keyed out on artificial characters, *Ellisia* has been recognized as a compound group consisting of section *Euellisia* Gray and section *Eucrypta* (Nutt.) Gray. The chief criteria employed by Nuttall (14) in founding *Eucrypta* as a genus were, first, its unique habit of bearing ovules upon both outer and inner faces of the placentae, and, secondly, the production of two very distinct types of seed in the inner and outer chambers thus formed. The subsequently discovered *E. micrantha* breaks down the second character because its seeds are homomorphic, but Brandegee's detection of the occasional presence of ovules on the side of the placentae away from the true locule has led to the association of this species with those which were known to Nuttall and included by him in *Eucrypta*. The fact that Bentham described *Ellisia* (*Eucrypta*) *chrysanthemifolia* as a congener of *E.* (*Euellisia*) *Nyctelea* without noting the presence of the "hidden" ovules and continued to maintain this position for the species even after this peculiarity had been pointed out, undoubtedly exerted a marked effect upon treatments by contemporary and later botanists.

The fruit and seed characters of *Eucrypta* are, in the writer's opinion, of more diagnostic weight than the presence or absence of appendaged calyx-sinuses in determining natural generic lines, as is admirably shown by the fluctuation of the auricle character within *Nemophila* and *Hydrophyllum*. Green (8) has adequately summed up the reasons for restoring *Eucrypta* to generic rank, in the following statement:

"These plants are not at agreement with *Ellisia* in habit. But if they were, capsules of such remarkable structure, and with seeds of two sorts so

strikingly dissimilar, neither sort answering to those of *Ellisia* or of any other Hydrophyllaceous genus, must, it seems to the writer, establish strongly enough a genus which was long ago well defined by an eminent authority. The name (meaning 'well hidden') is very admirably appropriate; for the pair of flattened seeds (rarely by the abortion of one ovule, solitary) which lie between the wall of the valve and its placenta, are so closely sealed as to have escaped the detection of that great botanist, the late Mr. Bentham, into whose hands one or both of the species fell at an earlier date than that of Mr. Nuttall's treatment of them, and who therefore described the plant as if it had been a real *Ellisia*."

In addition, the species which possess this peculiar condition of ovule formation also agree closely in their usually delicate habit, in the viscid and aromatic condition of their dissected, fern-like foliage, in the hispid pubescence, in their relatively complicated cymose inflorescence and in their narrow and rather shallowly divided calyx and corolla. Their distribution, chiefly in the arid portion of the southwestern United States, is comparable and suggests a common Mexican origin for the group. In the light of the foregoing arguments, the writer proposes to follow Nuttall (14), Greene (8), Heller (10, 11), Abrams (1) and Rydberg (16) in recognizing *Eucrypta* as a valid genus.

Because fruit and seed characters have been given so much weight in the genus *Phacelia*, and especially in the neighboring family Boraginaceae, the writer anticipated that something of value might be revealed by a comparison of the seeds of those species comprising *Ellisia* section *Euellisia* with those of *Nemophila*. The seeds of *Ellisia Nyctelea*, *E. membranacea*, *Nemophila aurita* and *N. racemosa* were found to be nearly globose and regularly reticulate or alveolate, and entirely devoid of any cucullus. Those of the remaining species of *Nemophila*, on the other hand, were mostly ovoid, smooth or tuberculate and variously pitted, but never either reticulate or alveolate, and always with a cucullus. The capsules of *Ellisia membranacea*, *Nemophila aurita* and *N. racemosa* are armed with stout prickles and bristles, a condition not duplicated elsewhere in the tribe Hydrophyllaeae. Furthermore, these three species agree in the possession of a peculiar scandent habit, the prickly armature of the stems and a closely comparable geographic range, which again points to a southern origin. These facts appear to confirm the suggestion that this group is a natural one. The close resemblance of the three species was intimated by Greene (9), who transferred *Ellisia membranacea* to *Nemophila* with the remark that this species is, "Thoroughly congeneric with *N. racemosa*; only empirically placed under '*Ellisia*,' notwithstanding the absence of calyx-bractlets." Similarly, Jepson (12), while restoring this species to *Ellisia*, referred to the same plant as, "In vegetative habit strikingly similar to *Nemophila aurita*."

The generic name *Pholistoma* was proposed by Lilja (13) with *Nemophila aurita* Lindl. as its type species. Although he based the genus chiefly upon minor characters, the name was effectively

published and a recognizable type species designated, so that it is available for further use. The writer proposes to take up *Pholistoma* for *Ellisia membranacea*, *Nemophila aurita* and *N. racemosa* (appropriate recombinations are to be included in a further paper on *Pholistoma*) because if they were thrown, collectively, into either *Nemophila* or *Ellisia*, because of their resemblance to certain species of each genus, the generic characters would be so weakened that *Nemophila* and *Ellisia* would have to be regarded as a single, unwieldy group, to be known henceforth by the Linnean name of *Ellisia*. Their segregation, it is believed, will achieve a more natural arrangement within the tribe, and free both *Ellisia* and *Nemophila* of discordant elements.

With the removal of section *Eucrypta* and the transference of one species to *Pholistoma*, *Ellisia* is restricted to the original species, *E. Nyctelea*, and so becomes a monotypic genus as it was known to Linnaeus. Its globose reticulate seeds are closely similar to those of *Pholistoma*, but it lacks the scandent habit, possesses a pubescent rather than a prickly stem, an unarmed capsule, and a very small, tubular-campanulate corolla. The predominantly temperate eastern American distribution of *Ellisia Nyctelea*, although outlying stations occur in the plains area of western Montana and of northeastern New Mexico, contrasts strikingly with the southwestern occurrence of *Pholistoma*, and indicates that the separation has been one of long duration. The fact that the corollas are narrowly campanulate and usually shorter than the calyx suggests an affinity, pointed out by Rydberg (16), with *Nemophila breviflora*, which, however, has quite different pitted and cucullate seeds, and with *Eucrypta*, which differs in its viscid herbage, more numerous flowers, weakly enlarging calyx, falsely pentalocular capsule, smooth or corrugated seeds and its widely different ecological and geographical range. The maintenance of *Ellisia* as a monotypic genus, then appears to be a satisfactory alternative to the dubious policy of including the very unlike species of *Nemophila*, *Pholistoma*, *Ellisia* and possibly even *Eucrypta* within the same genus. If all of these were merged, it would be exceedingly difficult to justify the exclusion of *Hydrophyllum* from the amorphous group which thus would be created.

Pollen morphology and chromosome number, it was hoped, might afford additional evidence as to phylogenetic relationships within the tribe. Preliminary and unpublished results seem to indicate, however, that a general similarity in microspore structure and in chromosomal complement prevails throughout the group.

The foregoing discussion can now be summarized in the form of a key to the genera as they are accepted by the writer, and which will be treated individually in revisionary papers which are either completed or in the course of preparation.

## KEY TO THE GENERA

- Perennial or biennial; leaves chiefly basal and all alternate; flowers numerous in scorpioid and often congested cymes; stamens exserted ..... 1. *Hydrophyllum* L.
- Annual; leaves chiefly cauline, at least the lowest pair usually opposite; flowers solitary or several in loose simple or paniced cymes; stamens included.
- Herbage variously pubescent, bristly, prickly or glabrate, but neither viscid nor scented; ovules borne only on the axial face of the placentae.
- Seeds lacking a cucullus, nearly globose and regularly reticulate or alveolate.
- Succulent, scandent herbs with prickly stems; corolla exceeding calyx; capsules armed with stout prickles or bristles ..... 2. *Pholistoma* Lilj.
- Flaccid herbs with hispid or glabrate stems; corolla exceeded by calyx or barely equalling it; capsules pubescent but unarmed ..... 3. *Ellisia* L.
- Seeds cucullate, mostly ovoid and smooth or tuberculate, often pitted and scrobiculate, but neither reticulate nor alveolate ..... 4. *Nemophila* Nutt.
- Herbage viscid and scented; ovules borne on both axial and abaxial faces of the placentae ..... 5. *Eucrypta* Nutt.

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